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Comparing Large, Infrequent Disturbances: What Have We Learned?

Monica G. Turner[1]* and Virginia H. Dale[2]

[1]*Department of Zoology, Birge Hall, University of Wisconsin, Madison, Wisconsin 53706; and* [2]*Environmental Sciences Division, Oak Ridge National Laboratory, PO Box 2008, Oak Ridge, Tennessee 37831–6036, USA*

The importance of natural disturbances in shaping landscapes and influencing ecosystems is now well recognized in ecology. Disturbances span a broad range of sizes and frequencies, and while understanding of relatively small disturbances has increased rapidly, the ecological effects of disturbance events that are large in spatial extent and infrequent in occurrence are not well understood. Examples of these large and infrequent disturbances include volcanic eruptions, big fires, and extreme floods or storms. Whether large, infrequent disturbances are qualitatively different from small frequent disturbances remains an unresolved issue in ecology, in part, because of a paucity of long-term data on the effects of broad-scale disturbances. The intensive postdisturbance research focused on several large natural disturbances (for example, the 1988 Yellowstone fires, Hurricane Hugo in 1989, the eruption of Mount St. Helens in 1980, and the 1993 floods in the Midwest) provides an opportunity to develop comparisons across these unusual events. The following set of articles begins to synthesize what is known about the ecological implications of *large, infrequent disturbances* (LIDs). In this article, we present the motivation for this synthesis by defining LIDs and discussing their ecological importance.

LIDs are difficult to define objectively because disturbances occur across a continuum of sizes and frequencies. We follow White and Pickett's (1985) definition of disturbance: "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment." This general but flexible definition requires the spatial and temporal scales of the system and the disturbance to be specified. Disturbances would typically be characterized by their size, spatial distribution, frequency or return interval, predictability, and magnitude, including both intensity and severity. Along the disturbance continuum, LIDs are much larger in spatial extent (terrestrial systems), or in depth/duration (floods) than the disturbances that "typically" affect the system. Rather than producing a rigid definition, we suggest two ways for identifying LIDs.

First, LIDs may be defined from statistical distributions of spatial extent, intensity, or duration. For example, the mean, median, and standard deviation of disturbance event characteristics can be used to characterize LIDs. Extreme flood events can be considered to be those in which water depth (stage) or flow volume (discharge, in cubic meters per second) is beyond 2 standard deviations of the mean for a period of record that spans at least several decades (Resh and others 1988). Since depth and flow vary seasonally in most rivers and streams, what constitutes an exceptional flood in one part of the year may be within 2 standard deviations of the mean during another season. The 1993 floods in the midwestern United States would have been major floods at any time of year, but the severity of their

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**Corresponding author; e-mail:* mgt@macc.wisc.edu

effects on floodplain vegetation was exceptional because they occurred during the summer growing season—normally the season of low, stable water levels. The floods lasted from late spring until fall, an unusually long duration for summer floods. Sustained flows that persisted for 120 consecutive days or more were well beyond 2 standard deviations of the summer average at many gauging stations (Southard 1995; Sparks and Spink 1998). Similarly, a frequency distribution of disturbance events can be used to identify LIDs. In landscapes affected by crown fires, a size–frequency distribution indicates that 1%–3% of fire events account for 97%–99% of the area burned (Bessie and Johnson 1995). Thus, these few fire events are both infrequent and very large. The statistics of extremes (Gaines and Denny 1993) also may be applicable to identification of LIDs.

Second, LIDs may be defined by perception of the event relative to a human scale or to the life span and attributes of the organisms in the ecosystem. For example, the 1980 eruption of Mount St. Helens was neither excessively large nor rare when considered in geologic time (Harris 1986), but it was both large and infrequent when considered from the perspective of humans and the organisms that inhabited the area. It is important to recognize that "large" may well be a function of the relative size of the organisms. For example, a storm-induced disturbance patch of 35–100 m^2 in the intertidal zone may seem small from the human perspective, but it is large relative to the organisms that reside there. What is considered infrequent also must be considered relative to the life span of the affected organisms.

LIDs are ecologically important because the imprint they leave on the ecosystem is large in area and may persist for a very long time. Indeed, a large disturbance event may even become the dominant force structuring the system, creating the template upon which subsequent ecological processes and interactions among species occur. Large crown fires in boreal forests, for example, create a mosaic of stands of varying ages that may persist for several centuries (Romme and Knight 1982). Volcanic eruptions create a spatial structure for vegetation patterns that may endure for millennia.

Although by definition they are large, LIDs do not result in extensive areas of uniform impact. Rather, LIDs create complex heterogeneous patterns across the landscape in which the disturbance may affect some locations but not others. For example, exposed ridges are more susceptible to damaging winds than are sheltered coves (Boose and others 1994), and even very large fires leave some stands unscathed because of wind shifts or natural firebreaks (Turner and Romme 1994). LIDs comprise areas affected by different disturbance intensities (Foster and others 1998) and have the potential to generate more heterogeneity than do small or weak disturbances. The LID-generated mosaic has important influences on biotic structure and ecosystem processes. Understanding the nature of these landscape patterns and the factors controlling them is essential for understanding and predicting ecosystem dynamics and vegetation development, and for developing guidelines for natural resource management.

LIDs may serve as catalysts for sudden and unexpected changes in ecological systems—there may be surprises or threshold effects that are only manifested following these extreme events. For example, LIDs may lead to the unanticipated recruitment of species or may increase the likelihood of alternative successional trajectories developing at a site [for example, see Abrams and others (1985)]. Ecologists need to understand the forces that may lead to such unanticipated changes across a landscape. Combining human and natural disturbances may also result in multiplicative effects. For example, large infrequent floods arise from natural causes, such as unusually heavy rains (for instance, the Midwest flood of 1993) or rain and rapid melting of unusually thick accumulations of snow (for example, 1997 floods in California and on the Red River in the Dakotas, Minnesota, and Manitoba). However, human alterations in the watershed, floodplains, and the rivers themselves contribute to well-documented trends of increasing flood heights for a given flow and increasing flood damage (Belt 1975; Leopold 1994; National Research Council 1995).

There are historical precedents for ecological studies of LIDs, but most early studies of large disturbances focused primarily on the effects of disturbance severity and did not consider the landscape perspective or the role of spatial heterogeneity. Cowles (1911) identified large disturbance as a factor responsible for changes in vegetation patterns. The importance of the pattern of the surviving biota for recovery of vegetation from volcanic eruption was studied by Griggs (1917). Clements (1916) also recognized the importance of such "residuals" for postdisturbance succession. However, prior knowledge still left ecologists unprepared to predict the effects of recent large disturbance events. In addition, the implications of LIDs for natural resource management have not been evaluated in an ecological context. The probability of occurrence of LIDs, their likely ecological effects, and whether or not they should (or can) be managed should be incorporated into environmental decision making (Dale and others 1998).

Much has been written about species that are adapted to either frequent or large disturbances (Grime 1977). Harper (1977) argues that the evolution of attributes that enable a species to respond to a disturbance relate to the frequency of the disturbance events relative to the life span of the organism of concern. The size of the disturbance also relates to the characteristics of species that inhabit a site. Areas that have experienced large, intense disturbances may contain early successional species that are highly dispersive and colonize from outside (Connell and Slatyer 1977), but this should not be assumed. For example, late successional species are known to invade a site very soon after a large disturbance (Dale 1991). This special section describes systems that have experienced disturbances that are both large and infrequent, but it does not explicitly deal with species adaptations.

LIDs are difficult to study and compare for several reasons. First, LIDs are usually unplanned and uncontrolled events. A single infrequent but large event is generally the focus of a study, and it is impossible to conduct truly replicated studies of LIDs. Replication usually occurs within areas of the disturbance rather than across disturbance events, inevitably leading to pseudoreplication. Furthermore, the areas affected by LIDs are generally not randomly distributed in space, and predisturbance data may be lacking or available only from small regions within the disturbed area. Second, studies of LIDs have never been formally coordinated, and available data vary in content and methodologies. For example, quantification of heterogeneity at the landscape scale has been done for some disturbances but not others; vegetation data may include herbaceous species in some locations but not others. Nonetheless, there are opportunities to replicate studies of the effects and processes associated with LIDs.

Eighteen ecologists gathered in May 1996 at the National Center for Ecological Analysis and Synthesis for a 2½-day workshop to compare and contrast what is known about LIDs. We were especially challenged to seek generalizations regarding their ecological significance, and our emphasis was on understanding broad-scale effects. Five synthetic papers emerged from the workshop and are included in this special issue, each addressing a particular aspect of LIDs across different disturbance types. First, Foster and others (1998) address the landscape patterns that result from LIDs, focusing on the factors that control these patterns and comparing disturbance-created mosaics by using recent disturbance events. Turner and others (1998) focus on the implications of LIDs for our understanding of succession and highlight lessons learned from studying LIDs. Romme and others (1998) consider the varied responses of ecosystems to disturbance to address the question “Are large, infrequent disturbances qualitatively different from small, frequent disturbances?” Paine and others (1998) examine the occurrences of major phase shifts, or bifurcations, in ecological systems that are associated with LIDs, especially when combined with other disturbances or chronic stresses. The final paper, by Dale and others (1998), explores the implications of LIDs for land and resource management.

Several terms are used repeatedly in these papers and are defined here for consistency. We use *severity* to describe the effects of the disturbance on the biota, rather than the energy released or force exerted by the disturbance, that is, disturbance *intensity* (although these are related). Disturbance severity is important in its own right; for example, hurricanes of the same spatial extent may have highly variable severities, which strongly influence ecological responses to these different events. The relationship between disturbance size and severity is complex. For some disturbances, especially floods and waves, duration is very important in determining severity. A key factor in severity of flood effects is whether flood duration exceeds the time it takes for flooded soil to become anaerobic and cause mortality of terrestrial plant roots.

When we discuss the *heterogeneity* created by LIDs, we refer to the spatial distribution of disturbance severities across the system. In comparing the ecological effects of LIDs, we discuss the legacies and residuals remaining after the disturbance. Ecological legacies of disturbance have both biological and physical components. *Biotic legacies*, or *residuals*, refer to the types, quantities, and patterns of organisms and biotic structures that persist from the predisturbance ecosystem. For example, residuals may include surviving individuals, standing dead trees, vegetative tissue that can regenerate, seed banks, litter, carcasses, and microbial and fungal soil community. *Abiotic legacies* are physical modifications of the environment that may result from the disturbance, for example, mass movements like mudslides or slope failures; lava flows; rocks or boulder movements during floods in high-gradient streams; channel and bank movement (rearrangement of the river and riparian zone); and silt deposition. Abiotic legacies may restructure the system. When considering LIDs, we are interested especially in the spatial distribution of these legacies in the affected ecosystems.

Ecologists and land managers will continue to be confronted by LIDs of various sorts, both natural and anthropogenic. The summer of 1996 saw some of the largest fires observed in regions of the southwestern United States, and the summer of 1997 saw extreme floods in California as well as the north-central region of the United States. The southeastern United States has been affected by several hurricanes in the past few years. This set of papers demonstrates that ecologists have indeed gained extensive knowledge about ecological responses to LIDs.

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